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PHYSIOLOGICAL OBSERVATIONS ON THE SUBTERRANEAN ORGANS OF SOME CALIFORNIAN LILIACEAE.

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(WITH PLATE XIV)

DURING my stay in the neighborhood of the Bay of San Francisco I have endeavored to get acquainted with the life-history of some of the numerous species of Liliaceae growing wild in that region, and my attention has been drawn especially to the physiological behavior of their subterranean organs. As the plants concerned exhibit some quite remarkable features, and have been little studied in this respect, and as they include some species of rather limited geographical distribution, I will give in the following pages an account of my investigations.

CLINTONIA ANDREWSIANA Torr.

The seeds of *Clintonia Andrewsiana* germinate in March. The cotyledon, after having absorbed the contents of the endosperm, serves as the first green leaf, growing 10^{cm} long and 3^{mm} wide. The primary root, 1^{mm} thick, reaches over 10^{cm} in length, and forms a few branches of the 1st degree. Its central cylinder is 3-archic, the endodermis with slightly thickened walls, the cortex starch-bearing. There are no signs of contraction. The stem develops into a rhizome, which grows almost vertically downwards to a depth of about 8^{cm}, where it passes over into the horizontal direction. Its annual prolongation is in young

specimens 1 to 3 ^{mm}, in adult ones 5 to 15 ^{mm}. Every year's formation may live over 20 years, so that the rhizome may attain a length of 15 ^{cm} and more. At first it forms yearly but one leaf; afterwards a stem 5 ^{cm} high with two leaves; finally a stem 12 ^{cm} high, crowned with about six leaves, and prolonged into the inflorescence. The leaves last very long, appearing above the ground in February and remaining green until October or November. The youngest portion of the rhizome develops every year, from October until April, the new roots being one or two in young, four to six in full-grown specimens. Their direction is downwards or sidewards. They are uniform throughout, without contraction, branch sparingly in the 1st degree, and are covered with root hairs. In adult specimens they are 2 ^{mm} thick, over 20 ^{cm} in length, and last about fifteen years. The central cylinder is 12-archic, its innermost part made up of thick-walled cells. The endodermis exhibits strong V-thickenings and thin-walled passage-cells in front of the hadrome rays, and there are no foldings on its longitudinal walls. The moderately abundant cortex is starch-bearing.

In Clintonia the roots are storing organs, but the rhizome is also rather rich in starch-bearing parenchyma. The roots have no influence upon the position of the rhizome. This latter grows downwards or upwards according to circumstances, and is sometimes very much curved.

PROSARTES HOOKERI Torr.

I found the seedlings of *Prosartes Hookeri* in the middle of April in an advanced state, yet still in connection with the seed. The germination probably takes place in March. The cotyledon, about 10 ^{mm} long, remains underground with its tip within the seed. The primary root, 0.75 to 1 ^{mm} thick, reaches over 10 ^{cm} in length, is uniform throughout, and branches in the first year sparingly in the 1st degree. It is provided with long root hairs. Its central cylinder is 9-archic, and the endodermis has slightly thickened walls. The cortical parenchyma is abundant and full of starch, and there is no contraction.

Immediately after germination the first aerial stem appears,

5–12^{cm} high, bearing two foliage leaves. There takes place the formation of a rhizome, which grows downwards, and elongates every year, at first 1 to 2^{mm}, later 3–5^{mm}, in adult specimens 5 to 15^{mm}. In old individuals it acquires a considerable length, comprising the formations of many years.

The head of the full grown rhizome produces yearly about five roots. These are 1 to 2^{mm} thick, over 20^{cm} long, uniform in all their length, or even increasing a little in diameter at some distance from the base. They run downwards and sidewards, wind very much from the start, and branch sparingly in the 1st degree. Their central cylinder is usually 18-archic, and made up in its innermost part of strongly thickened, very narrow cells. The endodermis has very strong, yellowish V-thickenings, and the adjacent two or three layers of the cortex are also somewhat thick-walled. The cortical parenchyma is abundant and contains starch. The epidermis forms long root hairs. Endodermis and hypodermis do not show any folding of their membranes. There is not the slightest indication of shortening of the root.

The rhizome of Prosartes is often very crooked. It may grow vertically upwards or downwards, according to circumstances. The roots have no influence upon its location.

Prosartes Menziesii Don. behaves just like *P. Hookeri.*

Fritillaria lanceolata Pursh.

The peculiarly shaped rhizome of *Fritillaria lanceolata* does not penetrate to a great depth. Its direction of growth is in young specimens sometimes inclined, in full-grown ones, situated 4 to 6^{cm} below the ground, horizontal. The yearly advance of the rhizome in horizontal direction amounts to 5 or 8^{mm}. Every new formation lasts but one year. There is a profuse vegetative multiplication, as larger specimens produce from 30 to 60 lateral bulblets. The plant brings forth yearly in younger specimens three or four, in adult ones about twenty thread-like roots, 0.5 to 1^{mm} thick and almost 10^{cm} long, branching in the 1st degree. The roots originate all at once, from one point, and run immediately in a horizontal direction. They have a

3-archic central cylinder and a thin-walled endodermis; both endodermis and hypodermis are without foldings. The roots are purely nutritive.

LILIUM PARDALINUM Kellogg.

In the gulches round Mount Tamalpais, where *Lilium pardalinum* grows in moist, shady places, I found the seedlings in an advanced state, but still connected with the seed, in the middle of April. The cotyledon, 5 ^{mm} long, remains underground, and its tip does not abandon the seed. Immediately after germination, however, a foliage leaf 4 ^{cm} high is formed. The primary root is 0.5 ^{mm} in diameter, furnished with hairs. Its central cylinder is 2-archic, the endodermis cells slightly thickened. The cortex is thin, and no signs of contraction are present.

The shoot develops into a bulb, the axis of which takes up a horizontal direction. The young plant produces every year but one foliage leaf and one to four fleshy scales; also the fleshy base of the foliage leaf, after withering of the blade, remains alive, functioning like a bulb-scale. In such specimens the bulb axis is about 3 ^{mm} long, and comprises but one year's product. It produces in the first periods two to four, later four to eight roots, originating exclusively from the lower side. Most of these roots are swollen at the base to 2 ^{mm} diameter, and shorten in this portion, so as to become wrinkled on the surface to an extent of 10 or 15 ^{mm}. As these contractile roots start from one point and grow almost vertically downwards, spreading away only by their ends, and as the bulb in the young individuals is very narrow, the latter is buried easily in the earth. Hence we find, while the seedlings are scarcely 1 ^{cm} below the ground, that half-grown specimens are 5 or 6 ^{cm}, full-grown ones 8 to 11 ^{cm} in depth.

At the time when the first aerial stem is brought forth the bulb axis is about 5 ^{mm} long, and produces about ten scales yearly. For full-grown individuals the annual prolongation amounts to 1 to 3 ^{cm}, and as a rule is horizontally directed. In this latter stage of development every year's formation lasts five

to seven years, and thus an old rhizome acquires a length of about 12^{cm}. Upon its upper side the rhizome bears the scars of the vanished aerial stems, each surrounded by a large number of bulb scales; at its basal end it is separated by a smooth scar from the dead portion. On its lower side the roots are found, five to twelve to each year's formation, starting rather close to each other. They are over 15^{cm} long, in their basal portion swollen to 3^{mm} in diameter, and branch rarely in the 1st, very rarely in the 2d degree. They live about five years, and grow from the beginning almost vertically downwards, but soon change their course into the horizontal direction. The swollen part is contractile, and becomes wrinkled to a length of from 5 to 20^{mm}. The central cylinder is 10-archic, the endodermis furnished with yellowish O-thickenings. In the active cortical parenchyma the cells of the innermost layers are radially elongated, those of the outer strata collapsed and compressed. Both endodermis and hypodermis show the radial longitudinal walls undulated. The epidermis bears root hairs.

In the thin, non-contractile end-portion, which otherwise has the same structure, the undulation of endodermis and hypodermis, the radial elongation of the cortex-cells, and the compressed cell-layers are wanting.

In the adult specimens, which have an ample growth of the horizontal rhizome and branch quite often, the roots apparently have no longer any considerable influence upon the position of the plant. I never found the position of the older parts disturbed. Specimens buried to an excessive depth are found sometimes growing up vertically and forming quite thin, smooth roots.

Scoliopus Bigelovii Torr.

Scoliopus Bigelovii grows in the shade of the redwoods, in moist, cool places. As is known, it flowers early in the year; in 1901 I found the last flowers at Mount Tamalpais at the end of February. By the prolongation and curvature of the stalks the ripening fruits are brought close to the soil, and there they open. I saw the first open fruits at the end of April. In many

instances I found seedlings and young individuals of different ages in dense patches at a distance of at most 30^{cm} from isolated mother plants. Owing to the length of the stalk the fruit can reach at most the distance of 15^{cm} from the center of the plant. There does not seem to exist any arrangement for the spreading of the seeds.

The seeds were found germinating in February. The cotyledon remains with its tips for some time in the seed, while its middle portion breaks above the ground by a knee-like curvature (*fig. 1*). Then it leaves the seed and stretches out, being the first green leaf of the plant. The primary root, 1^{mm} thick and beset with long hairs, reaches only 3^{cm} in length and does not branch. It has the central cylinder 2-archic, and a thick cortex. The latter becomes filled with starch-grains, except in the basal portion, where starch is almost absent; but here the undulation of the endodermis points to a slight contraction. After germination the diminutive stem of the seedling is at most 2^{cm} below the ground.

While the cotyledon dies down in the first summer, primary root and stem persist several years, the latter developing into a rhizome, the annual growth of which amounts at first to about 1^{mm} only. I do not know what the tendency of the rhizome may be regarding its direction of growth. The fact is, that the rhizome, in young specimens of normal, superficial location, assumes an almost vertically downward direction, with the growing point at the lower end (*fig. 2*). But this position, to a great degree if not exclusively, is due to the action of the roots. For the later roots, sometimes even the second one, shorten considerably, and as they all point more or less steeply downwards, they exert a pull upon the rhizome and drag it gradually deeper into the soil. However, as each root contracts only during the first months of its development, the older roots are out of action, and the pull is brought about only by the youngest ones, which arise from the growing end of the rhizome. This circumstance explains also the phenomenon that, while the youngest roots are quite straight, the inactive ones are (the older the more) curved

and bent down in their basal portions, apparently dragged by the movement of the rhizome to which they are attached (*fig. 2*).

The rhizome of old specimens is 3 to 5^{cm} long, comprising the products of twenty to thirty years, and is found at a depth of 5 to 7^{cm}. Here it has a horizontal direction, with an annual prolongation of 1 to 3^{mm}. It branches but rarely.

Young plants, which develop yearly only one leaf, form only one or two roots, while full grown specimens, as a rule, form three each year. The roots break forth all at once, in January or February. They may live twenty years, and therefore there are found sometimes forty to fifty of them on one plant. In older specimens the roots reach 20^{cm} in length, branch in their end-portion rarely in the 1st degree, and bear numerous root hairs. They are between 2 and 3^{mm} thick, their basal part, when quite young, being somewhat swollen to 3 or 4^{mm}. Central cylinder and cortex retain the same proportion throughout the root. The cylinder is mostly 8-archic, the rays being reduced somewhat in number towards the tips. The branches are 4-archic. The endodermis is made up of narrow cells with 0-thickenings and thin-walled passage-cells in front of the hadrome-rays. The cortical parenchyma is abundant and the hypodermis very distinct.

This being the general structure of the fully developed root, there are to be noted some differences between the basal portion and the more terminal one, which are related to the functions of these parts.

As already stated, each section of the basal region, soon after having finished its growth in length, begins to shorten. During this process, the active cells of the cortical parenchyma change their form, growing not only shorter, but also broader and becoming radially elongated. In this contraction and change of form, the epidermis, hypodermis, and two layers of cells bordering upon the latter — a complex, which we may designate as *passive outer cortex* — do not join. The outermost layers of the active cortex after a time collapse, are compressed by the expanding inner ones, and form a gradually broadening

zone immediately inside of the passive outer cortex. None of these changes appear in the terminal portion of the root.

Besides, there exists another difference, noticeable even in the primary root, but more pronounced in older plants. In that portion where the cells do not undergo any considerable change of form and size, the cortical parenchyma is densely filled with starch grains; but in the basal region, as far as the parenchyma exhibits strong activity of contraction, starch grains are entirely absent.

The contraction of the cortical parenchyma causes changes also in the passive tissues, inside as well as outside of it. Inside it leaves very characteristic traces in the endodermis. This tissue behaves like the elements of the central cylinder, becoming passively contracted in longitudinal direction. In the beginning, the cell-walls of the endodermis are straight and show nothing exceptional in their outer form, and so they remain in the end-portion of the root and in the branches throughout life. But in the basal portion, as far as contraction occurs, the radial-longitudinal walls of the endodermis become marked by an undulation running longitudinally. This undulation, here as in other species, corresponds to the dark spot, which is observed on the same wall on the cross-section. The undulation or wavy folding of the membrane is most pronounced near the root-base, where the strongest shortening takes place, and diminishes toward the root-end, being entirely absent near the tip.

Quite a similar phenomenon is to be noticed, outside of the active cortex, in the hypodermis. Also in this tissue, the membranes of which are quite straight at the beginning, as far as contraction reaches, an undulation of the radial-longitudinal cell-walls makes its appearance, becoming strongest in the basal region and diminishing and disappearing in the end-portion. The undulation of the cell-wall in both endodermis and hypodermis becomes fixed and remains nearly unaltered by separating these tissues in old roots from the adhering active parenchyma.

Some time after the appearance of the undulation, the pass-

ive outer cortex in its totality, in consequence of the shortening, loses its light connection with the active tissue beneath, becoming separated from it by the formation of the zone of compressed cells already mentioned. Hereupon the root-surface, tight and smooth at the beginning, becomes slack, rough, and wrinkled, and the whole root diminishes somewhat in thickness. The wrinkles begin to show themselves in March, when the roots are 6 to 10^{cm} long, still growing and without ramification. This wrinkled region, very insignificant in the first roots of the young plant, acquires in older specimens a length of about 2^{cm}.

TRILLIUM OVATUM Pursh.

Trillium ovatum lives in the same localities as Scoliopus, and also in its manner of life resembles this species in many respects. A difference of organization between both, noticeable even in the seedling, is that in Trillium the rhizome is used in a higher and the roots in a less degree as storing-organs than in Scoliopus.

I saw the germination already finished at the beginning of April. Seedlings and young plants of different age were found very often in the immediate neighborhood of the mother plant. While the cotyledon functions as the first foliage leaf, the stem of the seedling swells up to form a small tuber full of starch. The primary root, nearly 1^{mm} thick, reaching about 8^{cm} in length and forming a very few branches, contains but a small amount of starch grains, its central cylinder is 3-archic, the endodermis furnished with slight thickenings, remaining there as thin-walled passage-cells in front of the hadrome, the cortical parenchyma abundant, the hypodermis very distinct. There are signs of a feeble contraction in the root-base. Primary stem and root persist several years.

The second root, which in the following year breaks from the upper part of the tuber and grows vertically downwards, is considerably larger than the first one, has a thickened basal region, and exhibits there strong contraction, becoming finally wrinkled on the surface to an extent of 10 or 15^{mm}. In consequence of its

shortening it pulls down the tuber into a horizontal position, carrying with it also the basal part of the primary root.

The annual prolongation of the tuber amounts only to 1^{mm}, even in old specimens, but every year's addition broadens it, until in old tubers it comes to a permanent diameter of 10 to 15^{mm}. Such tubers are 3 to 4^{cm} long, containing the living products of twenty to forty years, and die off by degrees at the basal-end with a smooth scar. They do not branch. The full grown tuber brings forth on its lower side yearly two to four roots, situated close together and directed vertically downwards. The roots are about 30^{cm} long and 3 to 4^{mm} thick at the base, taper toward the tip, and branch there very sparingly in the 1st degree. They last about ten years, and twenty or more of them may be found attached to one tuber.

The central cylinder is 6-archic, the narrow-celled endodermis furnished with slight O-thickenings. The rather abundant cortex is almost devoid of starch grains in the swollen basal portion, but contains rather abundant starch in the thin terminal portion. The latter part of the root does not show anything extraordinary. The basal region, on the contrary, shortens very much, the active cortex cells elongating radially. As a result of the contraction, the radial-longitudinal walls of the endodermis become strongly undulated, a zone of compressed cells is formed below the outer cortex, and the root surface becomes wrinkled for a length of 3 to 5^{cm}.

The total shortening of the root probably amounts to about 10^{mm}. The main contraction goes on during the first months of the life of each root. Hence in Trillium, like in Scoliopus, mainly the youngest roots, situated nearest the growing end of the tuber, exsert a pull upon the latter. This pull brings it into an oblique, often vertical position, with the growing point at the lower end, so that the leaf stalk or the aerial stem forms a sharp angle with the rhizome. In this respect young specimens of Trillium and Scoliopus exhibit quite a similar appearance.

By degrees the roots drag down the tuber from the surface into the earth, so that old tubers are usually found 8 to 10^{cm}

below the surface. These latter, as a rule, are no longer inclined, but horizontal. I found here and there, however, always at a considerable depth, old tubers growing vertically upwards, with the roots starting equally from all sides. I am not quite sure about the conditions which provoke this kind of growth, nor about the tendency in the direction of growth the tuber may have in the other cases.

ZYGADENUS FREMONTI Torr.

Zygadenus Fremonti inhabits sunny, dry localities among shrubs, being very frequent in the chaparral. I found the young seedlings in great numbers in January (*fig. 3*). The cotyledon is subterranean; its tip, which is a well separated, roller-shaped sucker 3 to 4^{mm} long, remains within the seed; its lower part elongates downwards, burying the small stem 5 or 10^{mm} into the ground. A linear, upright foliage leaf, 5 to 10^{cm} long, is at once developed. The primary root grows about 6^{cm} long, and is remarkable for its swollen basal part, which is about 1.5^{mm} in diameter. Its central cylinder is 4-archic, the cortex extremely thick. The swollen part contracts a good deal, and thereby buries the stem still more into the earth. At the end of the shortening, we find the endodermis undulated, the active cortical cells radially expanded, a narrow ring of compressed cells formed in their circumference, and the passive outer cortex wrinkled to a length of 15^{mm}. The primary root branches but sparingly in the 1st degree, and is the only one formed in the first year. It dies off in the early part of May.

The shoot of the plant develops into a bulb and produces every year in younger specimens two to four, in the adult ones 10 to 15 roots. The roots originate at the beginning of the rainy season, in December or January, and die off at the beginning of the dry season; hence from June to November the bulb is rootless. They are all contractile, although in a different degree, and send out from the terminal region branches of the 1st and 2d order. In young specimens they always originate from one side of the bulb, so as to bring, by their

one-sided pull, the bulb-axis into an oblique position. In half grown specimens the roots acquire their greatest diameter, about 6^{mm}, and probably also the greatest amount of shortening, and drag the bulb every year 1 to 2^{cm} downwards (*fig. 4*). Their course is very characteristic, the contractile basal portion pointing almost vertically downwards, the inactive terminal portion passing into the horizontal direction. The central cylinder in these roots is usually 8-archic. In full-grown, old specimens, the growing point of which, as a result of the dragging of the roots, lies at a depth of 10 to 12^{cm}, the roots are thinner, at most 3^{mm} in diameter, start equally from all sides of the bulb-axis, and run in a flatter course (*fig. 5*). Their central cylinder has on an average nine rays, that of the branches three rays. In April, when the contraction is ended, the endodermis is furnished with exceedingly strong O-thickenings of yellow color, the hollow of the cells sometimes almost being filled up; but thin-walled passage-cells are present in front of the hadrome-rays. The cortex is copious. Root hairs are numerous. The bulb keeps, as a rule, a vertical position, elongates from 3 to 5^{mm} every year, and comprises the products of two years.

Remarkable are the differences between the contractile basal portion and non-contractile terminal portion of the root. For instance, the central cylinder preserves its diameter throughout its whole length, only the number of rays diminishing very little toward the tip; the cortex, on the contrary, is twice as thick in the basal region as in the terminal. Furthermore, the radial-longitudinal walls of the endodermis acquire, in consequence of the shortening, a strong undulation in the basal part of the root (*fig. 6*), whereas in the terminal part they do not show this peculiarity (*fig. 7*). Finally, the endodermis remains in the basal region thin-walled, until the contraction is finished, while in the non-contractile terminal region the thickenings make their appearance before that time.

CHLOROGALUM POMERIDIANUM Kunth.

Chlorogalum pomeridianum grows in dry, open localities, preferring rocky hills. In its manner of life it shows much resem-

blance to Zygadenus. Like the aerial organs, the roots also last only one vegetative period, sprouting at the beginning of the rains, in December and January, and dying off at the beginning of dryness in June or July.

Young seedlings were found in the latter part of January (*fig. 8*). The cotyledon is subterranean; its upper end, a globoid sucker, about 4^{mm} wide, remains in the seed, the rest elongates about 10^{mm} downwards, carrying the stem as far into ground. At the same time the first foliage leaf is sent forth, about 7^{cm} long with a blade 4^{mm} wide. The primary root, 1^{mm} thick and 5^{cm} long, develops near its end a few branches. Its central cylinder is 3-archic, the cortex moderately abundant. Its basal portion shortens, and in the thin walls of endodermis and hypodermis appears a heavy undulation. Besides the primary root, during the first year one or more roots appear, longer and gradually thicker, but in form and function equal to the first one.

From the second year onward a difference shows itself in the formation of these organs. At first from two to eight thin, thread-like, non-contractile roots are formed. They arc 0.5 to 1^{mm} thick, have a 4- or 5-archic central cylinder, and a moderately abundant cortex. After these, one or more roots appear, similar to those of the seedling, very thick in the basal region and tapering towards the tip, strongly contractile and growing vertically downwards (*fig. 9*). The largest of these I found were 10^{mm} in diameter, and were thicker than the bulb from which they arose. In these the central cylinder is 9–12-archic, the endodermis thin-walled, the cortex enormously abundant. The latter shows the radial elongation of the cells and a wide zone of compressed tissue (*fig. 11*). Both kinds of roots branch for a time in the 1st and 2d degree.

The work of thc contractile roots is considerable. The downward movement of the bulb was in several specimens 1.5^{cm} during one vegetative period. In this movement the bulb carries with itself the thread-like roots of the present year and also the dead but still adhering roots of the preceding year (*fig. 9*).

Thus, the growing point of the bulb, lying in the seedling 1 or 2 ^{cm} below the surface of the earth, is brought finally to the depth of 10 to 15 ^{cm}. There it is met, as a rule, in the full grown specimens, in which the bulb has attained a large size (*fig. 10*). An adult specimen produces about seven roots each year. Among these the difference in form and function disappears; they are all of the same kind, about 5 ^{mm} thick, tapering soon to 3 or 2 ^{mm} in diameter, and take up not a vertical, but more oblique course from the start. They are very long, covered with hairs, and form later on branches of the 1st and 2d degree. Their central cylinder is usually 13-archic, but the cortex reduced in abundance compared with that of the napiform roots of the half-grown specimens. The annual prolongation of the bulb-axis amounts in these old plants to 5 to 8 ^{mm}. So much are they carried down by the roots, however, that a full grown bulb, very superficially located, moved down in one year 2.5 ^{cm}.

In connection with the study of Chloragalum I should like to emphasize some facts concerning the behavior of the contractile roots. In Chloragalum, as in other species, the contraction does not appear in the whole root at once. On the contrary, as each section of the root a short time after having finished its growth in length begins to shorten, necessarily the older basal sections commence their contraction earlier than the younger, more terminal ones; also the phenomena accompanying the contraction appear sooner in the base. Thus we see in the napiform roots of Chloragalum that after a time the bark, smooth and light at first, becomes slack and wrinkled at the base, diminishing also in diameter, and that by degrees this wrinkling and falling down advances toward the tip over all the swollen basal region (*fig. 9*).

The roots of Chloragalum do not wait to commence their contraction until they have attained their entire length, nor do those of Zygadenus, Trillium, Lilium, Scoliopus, Arisaema, nor any other species I know of. On the contrary, in all these the contraction sets in when the roots are quite short, a few centimeters in length.

Neither do the roots of our plant wait to contract until they

have anchored themselves by lateral rootlets. On the contrary, when the few branches are formed, the contraction of the root is nearly or entirely finished. The same is true for the described species of Zygadenus, Trillium, Scoliopus, and likewise for *Calochortus umbellatus*, *Brodiaea capitata*, *Arisaema Dracontium*, and others. There are even contractile roots of a very strong dragging effect, which do not branch at all, as is the case in *Arum maculatum* and *Fritillaria Meleagris*. Apparently the close adherence of the root surface with the earth gives a sufficient support, and it seems even that in certain cases the presence of root hairs is not necessary for bringing about the effect.[1]

CALOCHORTUS UMBELLATUS Wood.

The bulb of *Calochortus umbellatus* is brought from the surface of the earth, where the seed germinates, to a considerable depth exclusively by the action of contractile roots. The bulb axis always grows vertically upwards, but not more than 1 or 2 ^{mm} a year, even in full grown specimens, in which the bulb is about 2 ^{cm} high and 1 ^{cm} thick. The whole plant renews itself annually, every part of it lasting but one cycle of vegetation.

At the beginning of the rainy season the bulb produces ten to twenty thread-like roots, 0.5 to 1 ^{mm} thick and 10 ^{cm} long, which give off numerous branches of the 1st and 2d degree. Those roots have the central cylinder 3-archic, a thin-walled endodermis, a moderately abundant cortex, endodermis and hypodermis straight-walled; they do not contract and are merely nutritive (*fig. 13 r*).

After these there appears one large napiform, contractile root (*fig. 13 r^1*.) It is in the basal portion from 2 to 4 ^{mm} thick, but is attenuated near the end to 0.5 ^{mm}. The central cylinder is 15-archic, and the cortical parenchyma copious. The active cortex cells elongate radially, their outermost layers collapse, and form a ring of compressed tissue bordering upon the passive outer cortex. The radial-longitudinal membranes of the thin-

[1] In regard to these details the descriptions of the phenomena concerned, as given in Kerner's *Plant Life* **2**: 769. 1891, and in MacMillan's *Minnesota Plant Life*, pp. 218, 219, 1899, are not exact.

walled endodermis become strongly undulated. After conclusion of the shortening, in April, this root ramifies sparingly. In larger specimens the root drags down the bulb 10 to 15 ^{mm}. By this movement the thread-like roots become displaced very much, and the bulb itself pulled out of the old husk, which sticks to the earth and remains in its place. The husks of several years sometimes persist, indicating the amount of work done by the roots in the respective periods (*fig. 13, h*).

Arriving at a depth of 6 or 7 ^{cm}, the plant stops the formation of contractile roots, producing then exclusively thread-like ones. In this state the new-formed bulb remains within the old husk, and at its bottom the remnants of the bygone bulb-axis accumulate, piled upon each other.

Brodiaea capitata Benth.

In full grown specimens of *Brodiaea capitata,* a species growing on sunny meadows, the subterranean part of the shoot is a tuber of vertical growth, rich in starch, about 15 ^{mm} thick, roundish, bearing on its lower end a round scar, the place where it was united with its predecessor. Its position is very superficial, only 3 to 5 ^{cm} below the ground.

It lasts but one year. In January, after starting the leaves, it begins to shrink and to become empty, but forms on its upper end a superposed new tuber. At the same time, from the base of the latter two pairs of lateral buds grow out, which likewise develop into small tubers, being supported by thin stalks about 1 ^{cm} in length (*fig. 14*). Each of these four lateral tubers is ensheathed by a fleshy sheathing scale, which later on dries up and becomes a brown husk. The stalks also die down, so that at the end of the rainy season the four small tubers are free, although still quite close to the mother plant.

The following year, at the beginning of the rains, mother and daughter tubers develop leaves and roots (*fig. 15*). The main tuber puts forth thirty to forty thin roots in a nearly horizontal direction, which become 10 ^{cm} long and sparingly branch. They have a 4-archic central cylinder with central vessel, endo-

dermis with feeble V-thickenings, and a narrow cortex. They show nothing peculiar, and are purely nutritive.

The daughter tubers, however, behave differently. After having formed two or three thin roots of the structure of those just mentioned, each of them sends out one thick, fleshy, contractile root (*fig. 15*, r^1). This root grows in a strictly horizontal direction, keeping in its whole extent not far from the surface of the soil. It reaches over 20^{cm} in length and 3 to 4^{mm} in diameter, tapering in its terminal portion to 1^{mm} in thickness. Its central cylinder is 5-archic with a central vessel, and the cortex is very thick.

It is semi-transparent, and it can be seen that the course of the central strand is not straight, but irregularly undulated and spiral (*fig. 16*). Such a course of the central strand is very uncommon in monocotyledons. Also in this case it seems to be not so much a necessary consequence of the shortening itself, as a consequence of the irregular manner in which the active cortical cells change their form. While in other roots the cortex behaves equally all around the central cylinder, in this case the radial elongation of the cells seems to take place now on one, now on the other side of the root, and the volume of the cortex increases alternately on different sides of the strand. This strange phenomenon, and the manner in which it is brought about, deserves a closer investigation. In consequence of the contraction the membranes of the thin-walled endodermis, as well as of the hypodermis, become undulated, and the root surface wrinkled to an extent of 3^{cm} from the base. No zone of collapsed cortical cells, however, forms. The anatomical peculiarities mentioned disappear near the tip.

The root seems to shorten about 10 or 20^{mm}. From every one of the lateral tubers the contractile root grows toward the outside, turning away from the mother plant. The result of the contraction is that every lateral tuber is pulled out of its husk, which remains on the spot, and is removed horizontally about 10^{mm} (*fig. 15*, t^2). During this process the small tuber, now in a horizontal position, shrivels and forms a new tuber on its top.

In the later part of the rainy season the emptied tuber-portion dies off with all the roots, and the following year the new tuber sends up its leaf about 1^{cm} away from the mother plant. The formation of horizontal contractile roots seems to repeat itself several times in the same individual.

This mode of loosening crowded colonies by the action of horizontal roots occurs, according to Kerner von Marilaun (*Plant Life* **2**:769. 1891), also in *Muscari racemosum* and *Ornithogalum nutans*. I have not yet had an opportunity of seeing it in these species. But it is by no means a frequent phenomenon, and does not occur at all in most of the bulbous plants, as Kerner assumes in the quoted passage. From my own experience, contractile roots of strictly horizontal direction seem to be very rare, and therefore their occurrence in Brodiaea is the more noteworthy.

Reviewing the ten species examined, we can state that, although they are geophilous herbs of similar organization, they nevertheless show extremely different modes of burying themselves. From this point of view we may arrange these plants in three groups:

The first group includes Clintonia, Prosartes, and Fritillaria. In these the rhizome alone, by its movement of growth, determines the location of the plant in the earth. It develops horizontally, and is not influenced in a mechanical way by the roots, which are not contractile.

The second group is formed by Lilium, Scoliopus, and Trillium. Here the growth of the horizontally developing rhizome determines in a much smaller degree the location of the plant. In general the influence of the contractile roots prevails in fixing the position of the rhizome.

The third group contains Zygadenus, Chlorogalum, Calochortus, and Brodiaea. In these the rhizome develops vertically, and the contractile roots determine almost exclusively the position of the plant.

Furthermore, we find that in Clintonia, Prosartes, Fritillaria, Lilium, Scoliopus, Trillium, and Zygadenus the roots are all of

the same kind and differ but slightly; whereas in Chlorogalum, Calochortus, and Brodiaea there takes place a division of labor between nutritive and contractile roots, accompanied by a striking difference in form.

Finally, considering the age the roots may attain, we see that it amounts to many years in Clintonia, Prosartes, Scoliopus, and Trillium, and to a few months only in Fritillaria, Zygadenus, Chlorogalum, Calochortus, and Brodiaea. Contractility is found not only in long-lived roots, but also, and in a very high degree, in short-lived ones. Long-lived roots assume also the function of storing reserve material; they may be contractile (Scoliopus, Trillium) or not (Clintonia, Prosartes). In those species which during a certain time of the year are rootless the roots never seem to be used as storing organs.

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EXPLANATION OF PLATE XIV.

All figures are drawn from nature, and where not otherwise indicated are natural size. The horizontal dotted lines indicate the surface of the earth. All the figures are in the natural position and distance with regard to these lines.

Scoliopus Bigelovii.

FIG. 1. Seedling: *s*, seed; *c*, cotyledon; *r*, root.

FIG. 2. Half-grown, descending specimen, at the end of January: *rh*, rhizome; *r*, fully developed roots of former year; r^1, new developing roots; *st*, aerial stem.

Zygadenus Fremonti.

FIG. 3. Seedling: *s*, seed; *c*, cotyledon; *l*, leaf; *r*, primary root.

FIG. 4. Half-grown, descending specimen, in February: *b*, bulb; *r*, contractile roots of the present year; r^1, remnants of roots of the preceding year, carried down by the movement of the bulb.

FIG. 5. Bulb of full-grown specimen, in March; longitudinal section: *a*, bulb-axis; *st*, aerial stem of the present year; st^1, aerial stem of the preceding year; *r*, contractile roots.

FIG. 6. Endodermis from the basal portion of a contractile root; tangential section. $\times$ 200.

FIG. 7. Endodermis from the terminal portion of the same root; tangential section. $\times$ 200.

Chlorogalum pomeridianum.

FIG. 8. Seedling: *s*, seed; *c*, cotyledon; *l*, leaf; *r*, primary root; r^1, second root.

FIG. 9. Half grown, descending specimen, in the latter part of January: *b*, bulb; *r*, non-contractile roots; r^1, contractile root of the present year, with the wrinkles appearing at the base; r^2, dead, contractile root of the preceding year, pulled downwards by the movement of the bulb.

FIG. 10. Lower portion of adult bulb; longitudinal section: *a*, bulb axis; *bs*, bulb scales; *st*, aerial stem of the present year; st^1, remnants of the aerial stem of the preceding year; *r*, living root of present year; r^1, dead root of preceding year.

FIG. 11. Cross-section from the basal portion of a contractile root of a young, descending specimen, $\times 5$: *cyl*, central cylinder; *in*, inner (active) cortex; *com*, layer of compressed cells; *out*, outer (passive) cortex.

Calochortus umbellatus.

FIG. 12. Young, descending specimen, in April: *b*, bulb; r^1, contractile root; *h*, husk of the last year.

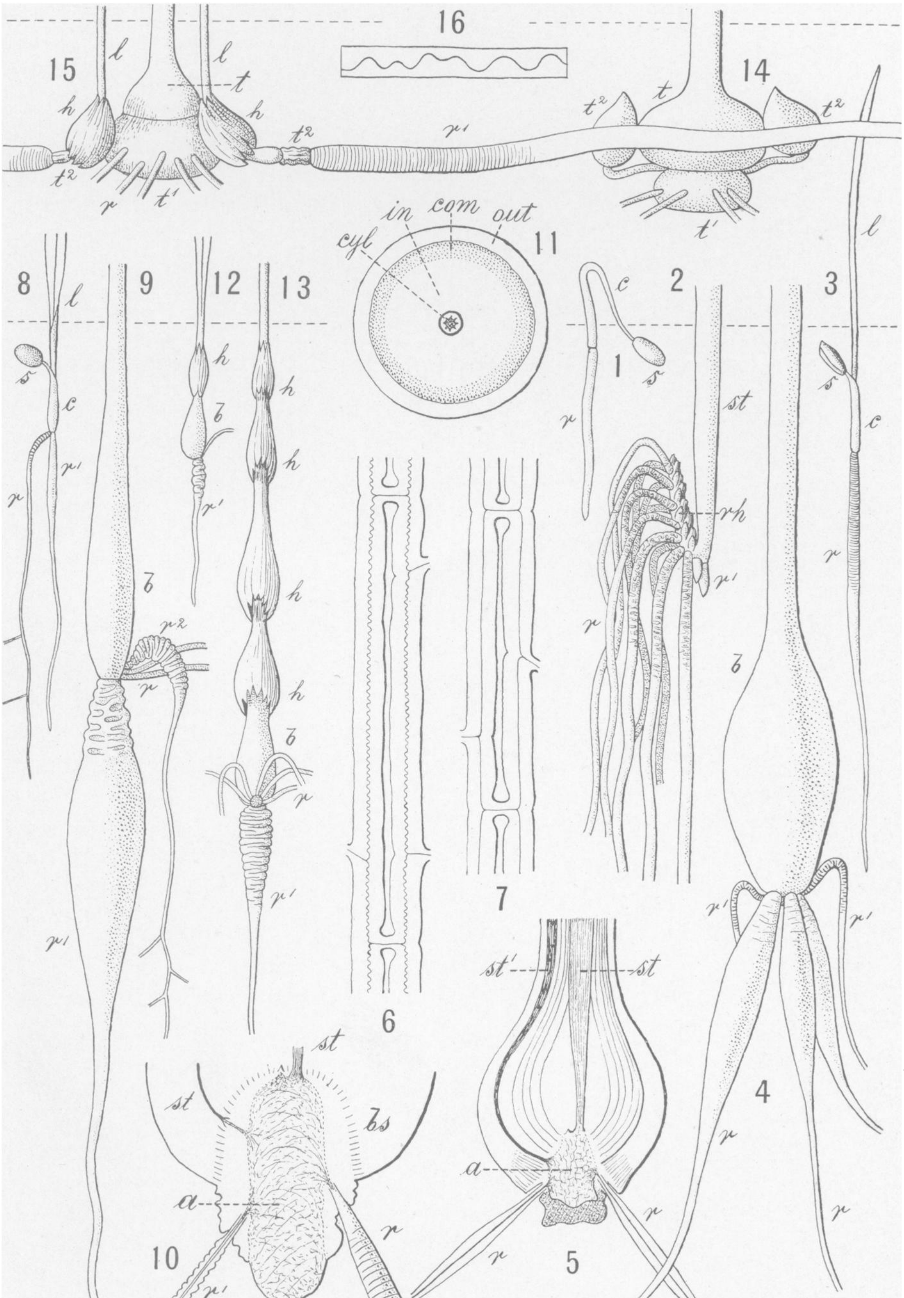
FIG. 13. Almost full grown, descending specimen, in April; the contraction is finished: *b*, bulb; *r*, non-contractile roots; r^1, contractile root; *h*, dead husks of preceding years.

Brodiaea capitata.

FIG. 14. Subterranean parts in March: *t*, newly formed part of main tuber; t^1, old, decaying part of the same; t^2, new, lateral tubers fully developed.

FIG. 15. Subterranean parts in January: *t*, new part of main tuber in formation; t^1, old part of main tuber; t^2, last year's lateral tubers, shriveled and carried away from the mother plant; *h*, dry husks of the same; *l*, leaves of the same; *r*, thin roots of main tuber; r^1, contractile root of lateral tuber.

FIG. 16. Piece of contractile root, showing course of central strand. $\times 2$.



RIMBACH on SUBTERRANEAN ORGANS